BEYOND HIGH QUALITY HABITAT CORRIDORS:

EVALUATING THE EFFECTIVENESS OF

REALISTIC ALTERNATIVES

By

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Abstract: Increasing connectivity between habitat patches remaining from anthropogenic land conversion is known to mitigate the effects of habitat fragmentation. This is often implemented through corridors, linear strips of habitat that connect larger habitat patches surrounded by a non-habitat matrix. Typically corridors are created of the same "high-quality" habitat as the isolated patches they connect; however, this may not always be feasible. We used a model system approach to assess the efficacy of lower-quality habitat corridors for increasing dispersal. Using isopods as a model organism, we used coco fiber to create a standard corridor study design. Habitat patches and high-quality corridors were supplemented with food and kept at high moisture levels favorable to isopods. Low-quality corridors lacked food and had lower moisture levels. We placed 125 isopods under each release patch, and counted the number of isopods in each patch and corridor for eight days. Mean isopod counts did not significantly differ between target patches connected with high- or low-quality corridors ($Z = -0.359$, $p = 0.720$), high quality and low quality corridors differ in isopod presences ($Z = -1.541$, $p = 0.123$) . Infrequent use of the model system may be due to extreme climatic conditions (e.g. temperature, light intensity), causing isopods to leave the study system for more favorable conditions.

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CHAPTER I

BEYOND HIGH QUALITY HABITAT CORRIDORS: EVALUATING THE EFFECTIVENESS OF REALISTIC ALTERNATIVES

Anthropogenic conversion of natural habitat occurs on a global scale and is considered the most prominent threat to biodiversity (Wilson 1988). One serious effect of conversion is habitat fragmentation, which includes the breaking apart of a large contiguous tract of habitat into small, isolated fragments, as well as the loss and degradation of that habitat (Sawyer et al. 2011). In areas with high levels of habitat fragmentation, the matrix (the non-habitat area surrounding habitat patches) is often the dominant patch type in a landscape. The effects of habitat fragmentation are numerous, as well as the factors that influence how detrimental habitat fragmentation can be, such as the permeability of the matrix. I discuss these numerous effects and influencing factors throughout the remainder of this paper, beginning with the initial effects of habitat fragmentation and conversion. I then discuss how the matrix and edge boundaries can influence dispersal throughout the landscape and how low dispersal between habitat fragments can negatively affect populations. Habitat use, species composition, and population dynamics are also altered through fragmentation, including increases in predation. These elements are partly

caused by edge effects, which in addition to influencing an organism's likelihood of leaving an isolated patch, can influence abiotic factors within the patch and whether or not the patch acts as an ecological trap. Finally, I discuss how the effects of habitat fragmentation contributed to the application of the theory of island biogeography to terrestrial habitat patches and additional connections to metapopulation theory. This context is important because of the relevance of these concepts to conservation management practices, such as increasing the movement of individuals among isolated patches through the addition of corridors and/or stepping stones.

Perhaps the quickest and most obvious effects of fragmentation are the initial displacement and mortality of organisms, crowding effects, and reduced resource availability. Initially after fragmentation, populations may increase due to being displaced from their original habitat (Noss 1981). However, this initial increase is often followed by population collapse (Debinski and Holt 2000). Fragmentation may also lower the amount of microhabitats and resources available to organisms (Parker and Mac Nally 2002). If additional habitat is not available, or if a species has poor dispersal capabilities, the population (or even species) may be susceptible to extinction. Endemic species may be especially susceptible if they are narrowly distributed. Some fragments may be smaller than the home range of species, or some species may avoid small patches with high amounts of edge (e.g., interior specialists) (Lehtinen et al. 2003). However, fragmentation may increase the abundance of some species, particularly predators and parasites (Lehtinen et al. 2003). Examples of increased abundance of predators and parasites along edges include small mammals (e.g., red squirrel), larger carnivores such as foxes (Andren and Angelstam 1988), and nest parasites such as the brown-headed cowbird (Brittinghman and Temple 1983).

The mobility of a species and spatial scale at which that species perceives the environment can influence the degree to which the matrix facilitates or impedes movement. For example, some non-volant insect species may perceive a road through the forest as an impenetrable barrier, while a bird may easily cross this gap (Forman et al. 2002, Lindenmayer

and Fischer 2006). The structure of the matrix relative to the structure of habitat is also a key factor that affects dispersal (Laurance et al. 2002). If the vegetation structure of the matrix is similar to that of an organism's habitat, some species may readily cross habitat-matrix boundaries and the matrix may facilitate movement between habitat patches (Noss and Cooperrider 1994). However, when the structure of the matrix differs substantially from the habitat, some species may be less likely to cross the habitat-matrix boundary and the matrix may then function as a barrier to movement. In one study, 4 out of 6 butterfly species were more likely to move between meadow patches (i.e., habitat) when the matrix was comprised of willow forest instead of conifer forest (Ricketts 2001). In addition, the permeability of the boundary of the habitat patch can influence immigration and emigration. A boundary would be considered "hard" if dispersing individuals rarely cross the boundary to move to surrounding habitats (Stamps et al. 1987). In contrast, habitat patches can be bounded by a soft edge –one that is permeable to emigrating organisms, when individuals frequently cross the boundary to move to surrounding habitats. Whether an edge is perceived as soft or hard is species specific (Stamps et al. 1987).

Isolation of habitat can threaten the persistence of populations in numerous ways. Smaller and more isolated populations are at greater risk of being negatively affected by environmental and demographic stochasticity (Keller and Waller 2002, Sawyer et al. 2011). When the isolation of habitat patches is greater (i.e., greater separation distances or harsher matrices), immigration rates will be lower, the probability of extinction will be greater, and the chance of recolonization will be lower (Gibbs and Stanton 2001). Lower immigration rates may lead to inbreeding depression and genetic drift, both of which can increase the probability of extinction (Leidner and Haddad 2011). While increased mortality associated with genetic factors caused by inbreeding may not be seen frequently, inbreeding can increase individual susceptibility to death from environmental factors (Keller and Waller 2002). For example, Saccheri et al. (1998) found that inbreeding of the Glanville fritillary butterfly in Finland significantly increased the extinction risk of populations through effects on larval survival, adult life expectancy, and egg-hatching rates.

Fragmentation can alter numerous ecological processes such as habitat use, species composition, and population dynamics (Karsai and Kampis 2011). Predation may increase in the matrix. This may reduce movement rates between habitat patches for the prey species (Collinge 2000). One study found that habitat fragmentation effects in carrion beetle communities resulted in a species richness reduction of one-third and abundance reduction of two-thirds when compared to communities in contiguous forest (Gibbs and Stanton 2001). Fragmentation can also influence interspecific interactions. For example, Gibbs and Stanton (2001) found a reduction in abundance of carrion beetle predators, flies, and commensal mites.

Increased levels of edge can have various impacts on species. For instance, the amount of light that reaches plants is higher at the edge of the habitat than in the interior, as are wind velocities (Collinge 1996). This leads to increased temperatures at edges as well as decreased relative humidity. In Douglas fir forests in the Pacific Northwest, there were increases in the amount of trees uprooted by wind and reduced humidity levels that could extend over 200 meters beyond the edge (Chen et al. 1990). These abiotic factors not only influence the plant and animal communities that live at the edge, but also can influence those within the interior of the patch. For example, alterations in microclimate near edges reduced seed germination and seedling density in an understory herb (Tomimatsu and Ohara 2004). Plant communities may change as a result of the differences in abiotic factors. Ranney et al. (1981) found that forest edges, when compared to interior forest patches, contained more xeric and pioneer plant species with higher densities of shrubs and herbaceous groundcover. As edge increases, the amount of suitable space for interior habitat dwelling species decreases (Parker and Mac Nally 2002). Edges may also act as an ecological trap with increased predation or parasitism rates. For example, rates of nest predation from opportunistic predators (e.g., crows, skunks, foxes) may be concentrated around edges and extend hundreds of meters from edges (Wilcove 1986). Edges may also attract animals, such as in Michigan where passerine birds were attracted to a field-forest edge and were found to nest at greater densities than in the forest interior. However, passerine birds experienced increased levels

of predation and brood parasitism from Brown-headed cowbirds, which resulted in reduced fledgling success (Gates and Gysel 1978).

As the effects of habitat fragmentation became apparent, a relationship between habitat patches and the theory of island biogeography developed. The theory of island biogeography from MacArthur and Wilson (1967) was originally applied to oceanic islands and identified factors that influence species richness on islands. For instance, isolation affects immigration and colonization rates. As the distance between the island and the mainland increases (the greater the isolation of the island), the fewer the species found on that island (MacArthur and Wilson 1967). This is because fewer species can disperse to distant islands, lowering immigration rates and reducing the likelihood of population persistence. Area also affects colonization rates. When the area of an island increases, there is a greater chance that a dispersing organism will encounter and colonize the island (MacArthur and Wilson 1967, Shafer 1990). Larger islands also tend to contain more microhabitats than smaller islands (providing more niches), allowing for a greater number of species to persist (Haila et al. 1983, Rosenzweig 1995, Lindenmayer and Fischer 2006). When applied to fragmented habitat on land, the habitat patches correspond to islands and the matrix corresponds to the ocean. As patches become further isolated from the main source of colonizers (i.e., the mainland in island biogeography), extinction is likely to increase as a patch is less likely to receive immigrants to "rescue" smaller, local populations from extinction (Brown and Kodric-Brown 1977, Lomolino 1996, Collinge 2000, Watling and Donnelly 2006). When patches are closer together, immigration rates should be higher than extinction rates, decreasing the probability of extinction (MacArthur and Wilson 1967).

Another ecological theory that applies to habitat fragmentation is metapopulation theory (e.g., Hanski et al.1995, Hanski 1998, Fullerton et al. 2011). A metapopulation is a set of subpopulations of the same species separated by space or barriers, and linked by occasional dispersal (Levins 1970, Gilpin 1991, Collinge 1996). As defined by Levins (1970) a

metapopulation is "a population of populations." Before metapopulation theory was applied to conservation biology, the theory was developed to describe the population dynamics of species living in naturally patchy habitats (Hanski and Gilpin 1991). Local populations go extinct and patches are recolonized over time (Stacey and Taper 1992, Hanski 1999). Vacant patches are likely smaller and/or more isolated than occupied patches (Collinge 2000). Although small, local populations may go extinct, the metapopulation as a whole persists (Harrison 1991, Hanski 1999).

The theory of island biogeography and metapopulation theory contributed to viewing isolated habitat patches as islands for conservation purposes (Haddad 1999). Increasing connectivity of habitat patches can mitigate the effects of fragmentation (Chishom et al. 2011, Leidner and Haddad 2011). Connectivity can be defined structurally or functionally (Tischendorf and Fahrig 2000). Structural connectivity is defined as the physical connectedness of the landscape (i.e., direct connections), and does not take into consideration how organisms perceive the landscape (Tischendorf and Fahrig 2000, Lindenmayer and Fischer 2006). Functional connectivity refers to how connected a landscape is from an organism's perspective, and therefore differs among species for the same landscape. Both theoretical and experimental studies where structural connectivity of habitat patches has been increased have shown an increase in the likelihood of population persistence (Chisholm et al. 2011).

Corridors and stepping stones are a popular means of increasing connectivity between patches of habitat (Hess and Fischer 2001). Corridors are continuous linear strips of habitat that connect larger patches of habitat surrounded by a non-habitat matrix (Forman 1995, Bennet 1998). Typically, corridors consist of the same quality of habitat as the patches they connect (e.g., tall grass prairie patches are connected by tall grass prairie corridors). Stepping stones are like corridors in that they connect larger patches of habitat surrounded by a non-habitat matrix, but they are smaller, non-continuous patches instead of one linear strip (Forman 1995, Lindenmayer and Fischer 2006). If an organism will cross patch-matrix boundaries, stepping stones may be a

good alternative to corridors. Stepping stones may also be more effective at increasing connectivity for some species, such as volant species or those whose native habitat is originally patchy (Date et al. 1991, Schultz 1995, Bennett 1999). Stepping stones are also typically composed of the same quality habitat as the patches they connect. While corridors and stepping stones should not be seen as a substitute to preserving areas of high quality habitat, they can be useful conservation tools to increase the habitat available to a species and movement among habitat patches (Haddad and Tewksbury 2005).

The intended function of corridors is to increase the movement of individuals among isolated habitat patches, thereby increasing gene flow and immigration rates (Collinge 2000, Haddad and Tewksbury 2005). With the increased movement of individuals, small populations can be rescued from extinction through reduction of inbreeding and genetic drift (Haddad and Tewksbury 2005), reducing variability in birth and death rates, and increasing the probability of patches becoming re-colonized (Rosenberg et al. 1997). Corridors do not have to maintain the same movement rates as the contiguous habitat prior to fragmentation, as even minimal dispersal between patches can mitigate genetic loss (Gilbert-Norton et al. 2010). Several studies have shown that corridors are meeting their intended function of increasing connectivity through increased population sizes, gene flow between patches, and movement between patches (Beier and Noss 1998, Haddad and Baum 1999, Mech and Hallet 2001). Beier (1993) observed through modeling studies that even a small number of cougars dispersing was sufficient to improve the chances of survival for a cougar population in southern California. A meta-analysis of corridor studies found that there was 50% more movement between habitat patches that were connected by a corridor than between isolated habitat patches (Gilbert-Norton et al. 2010). In one large-scale experiment, two butterfly species were found to move more frequently between habitat patches connected by a corridor than those that were not (Haddad 1999). The study also found that as the distance between habitat patches increased, movement between connected habitat patches increased (relative to unconnected habitat patches at similar distances) (Haddad 1999). Beier and

Noss (1998) reviewed corridor studies, and they found that in almost all studies included in the analyses, corridors showed a benefit to organisms in real landscapes.

METHODS:

Model System Approach:

Using model systems has become a common approach for testing ecological theory. Model systems in ecology typically consist of organisms that are abundant, easy and inexpensive to work with, and that respond to the environment at small spatial scales (Srivastava et al. 2004). Model systems can control for many environmental variables that may influence results such as competition and predation, as well as abiotic factors such as temperature and precipitation. Landscape level studies require large scale manipulations, which can be costly and logistically difficult. Using a model system provides information and insight into possible effects and results without manipulating a larger area of land. Identifying correlations between the life history traits of model species and species of conservation or management concern can provide the context for extending the implications of small scale, model system studies to larger scale issues, such as evaluating alternative management strategies for nature reserves (Grosholz 1993, Rantalainen et al. 2004, Lawton 1999). The same factors that influence the responses of model species to landscape structure, such as the probability of crossing habitat boundaries or behavior at edges, is likely similar for more difficult to study species that function at larger spatial and/or temporal scales, and for which corridors are often proposed to increase connectivity (Haddad et al. 2000). Considering scale and factors such as dispersal capabilities and generation times can aid in extrapolating results from the model system to other systems (Rantalainen et al. 2006).

Isopods as a Model System:

The effects of habitat fragmentation and corridor use have been studied numerous times using invertebrates as part of a model system. For instance, grassland insects were used to assess how spatial arrangement of habitat patches influences species composition (Collinge and Forman 1998). Another study assessed how patch use by butterflies and skippers was affected after habitat fragmentation (Summerville and Crist 2001). Which characteristics of corridors provided beneficial effects were determined using microarthropods (e.g., mites, springtails, pseudoscorpions) in a microecosystem (Hoyle 2007). In another study, a model system with planthoppers was used to assess how altering the resistance levels of the matrix influenced dispersal through stepping stones and corridors (Baum et al. 2004).

Several studies have evaluated the effects of fragmentation on isopods, in addition to using them as a model organism. For example, isopods were used to assess the effects of a virus on intra- and interspecific competition as well as how competition influenced infection rates. Through using isopods, Grosholz (1992) found that interspecific interactions produced higher virus prevalence than intraspecific interactions. In another study, Grosholz (1993) used isopods to examine how spatial heterogeneity and patch separation distance influenced the dynamics of host-pathogen populations. Natural isopod populations showed a seasonal increase in patchiness and inter-patch spacing that was accompanied by a seasonal decrease in virus prevalence, even in situations were within-patch isopod densities increased. Isopods were part of an urban habitat fragmentation study by Bolger et al. (2000) in southern California examining how non-ant arthropods may be affected by edge effects, and they found that arthropods showed an effect of fragmentation with diversity and abundance positively correlated with fragment area and negatively correlated with fragment age. Isopods have also been studied in fragmented forests to determine how fragmentation affects their populations as well as species richness (Tajovsky et al. 2012). Isopod species *Armadillidium vulgare* and *Protracheoniscus politus* had greater abundances in larger fragments of woodland. Finally, isopods have been used as indicators of environmental quality; however, further work is needed to determine how well they represent

environmental quality (e.g., soil contamination) in comparison to other taxa, such as earthworms and carabid beetles (Paoletti and Hassall 1999).

Isopods are arthropods that can be found in both terrestrial and marine environments. Most isopods are omnivores and typically feed on detritus (decaying plant and animal matter), fungi, and living plants (Warburg 1993). Isopods will also cannibalize their own young and other injured or molting isopods (Grosholz 1992). They are globally distributed, in large part due to human activity (Grosholz 1992). They can live at least four years, reaching maturity after one year, and may produce three broods per year during the spring and summer (Grosholz 1992). Dispersal and abundance of isopods are highly influenced by soil moisture, as well as temperature, humidity, and light intensity (Warburg 1993). When humidity is low, isopods select moist microhabitats, such as the upper layer of soil, leaf litter, under stones, and the bark of trees (Warburg 1993). Most mortality of isopods is due to climatic factors such as drought or high temperatures, although their primary predators are other arthropods, such as arachnids (Warburg 1993). While isopods are most active during warmer months, high temperatures or drought can reduce activity levels. They are nocturnal and will remain inactive or hidden during the day to prevent water loss. Isopods are typically abundant, easily identifiable, and a dominant component of detritivore communities in many regions (Warburg 1993, Hornung et al. 2007).

Objectives: My two objectives for this study were to: 1) Evaluate the effectiveness of low quality corridors for increasing connectivity, and 2) Evaluate how altering the spatial scale of habitat patches and corridors affects dispersal. Results from these objectives provide greater insight into possible alternatives for increasing connectivity, including the implications of spatial scale, and inform the development of conservation strategies and management decisions.

Objective 1: Evaluate the effectiveness of low quality corridors for increasing connectivity. Corridors typically consist of the same habitat as the habitat patches they connect, and for this

reason can be considered “high quality”. High quality corridors may not always be feasible and alternative types of corridors may increase the conditions under which corridors can be used to increase connectivity between habitat patches. An alternative type of corridor could be one that does not consist of the same high quality habitat as the patches they connect, but could be considered less hostile than the matrix, and therefore a “low quality” corridor. The presence of a low quality corridor could also increase the probability of an organism leaving a high quality patch compared to if the patch were isolated and completely surrounded by matrix. Lower quality corridors may increase dispersal between habitat patches compared to high quality corridors, since an organism may be less likely to remain in a low quality corridor or may move more quickly through a low quality corridor than a high quality corridor. High quality corridors may be considered habitat by some organisms and act as ecological sinks due to edge effects (e.g., increased predation rates from matrix dwellers, higher levels of competition from generalist species; Hess and Fischer 2001). Even if dispersal rates are lower in low quality corridors than in higher quality corridors, they can still be an effective alternative, as even minimal dispersal between habitat patches can alleviate the loss of genetic diversity (Norton et al. 2010).

I used the isopod species *Armadillidium vulgare* (Class Isopoda, Subphylum Crustacea, Phylum Arthropoda) as a model organism to examine the efficacy of low quality corridors for increasing connectivity (e.g., Grosholz 1992, 1993). Grosholz (1993) created artificial habitat patches using dampened straw bales, which provided a suitable microclimate for the desiccation sensitive isopods. He determined that dispersal rates between straw bale habitat patches and natural habitat patches of *Eriophyllum staechadifolium* were similar, indicating that straw bales can be used to mimic natural habitat patches. In another study, Grosholz (1992) used fiber mats as habitat patches, which were also periodically dampened to maintain a moist microhabitat. Grosholz found that watered coco fiber mats were effective in recruiting isopods from the surrounding landscape (mean = 348.8 isopods/m^2, range 178-518 isopods/m^2), indicating that watered fiber patches can sustain an isopod population and are representative of natural

conditions for isopods. I used coco fiber mats since they are easier to manipulate (i.e., create corridors of a selected size) than straw bales and isopods are likely easier to find and count.

I created an experimental landscape design similar to the one used by Baum et al. (2004). Each experimental landscape consisted of a central release patch and three target patches, placed 2.5 m from the central source patch. Grosholz (1993) found moderate isopod dispersal at this distance (compared to very high dispersal among patches separated by 0.25 m and low dispersal among patches separated by 10 m). All patches were 0.36 x 0.36 m^2, a size used in a previous experiment by Grosholz (1992). Target patches were connected with a low quality corridor, a high quality corridor, or nothing (i.e., isolated to serve as a control) (Figure 1). The orientation of these patches was randomly determined in one of the four cardinal directions for each replicate landscape. Corridors were 0.13 m x 2.5 m and consisted of the same coco fiber mat material as the habitat patches. The width of the corridor was partially determined based on the width needed for the coco fiber material to stay intact (13 cm).

The treatment with the isolated/unconnected habitat patch served as the control to evaluate if isopods would disperse through the intervening matrix without using a corridor. The next two treatments consisted of habitat patches connected to the release patch by corridors. The corridors were manipulated so that they would consist of a higher or lower quality of habitat, based on the moisture and dietary requirements of isopods. The “high quality” corridor treatment served to mimic the standard corridor study design, with the corridor consisting of the same high quality habitat as the patches (i.e., both food resources and an appropriate microclimate for the isopods). The "low quality" corridor treatment consisted of a target patch connected to the source patch with a low quality corridor. All patches (one release and three target) and corridors (high quality and low quality) were watered with a backpack sprayer to increase the moisture levels compared to the matrix. All patches and high quality corridors were watered daily so that the average soil moisture readings fell within the range of 8-10 on the soil moisture meter (Lincoln) at 2 cm, 4 cm, and 6 cm below the surface. The soil moisture meter provided values between 0

and 10, 0 indicating that there is very little to no moisture in the soil, and 10 representing saturation. The patches (release and target) and high quality corridors also received carrots and potatoes as a food supplement. Since isopods are omnivores, carrots and potatoes are an adequate supplemental food source. Carrots and potatoes were weighed in equal proportions and placed under the patches and high quality corridors at the beginning of each trial. Low quality corridors were created with the same coco fiber mat as the habitat patches and high quality corridors, but received less water than the patches and high quality corridors, and did not contain supplemental food. Low quality corridors were watered so that they maintained moisture readings of approximately 5-7. Therefore, these corridors were lower in quality than the habitat patches and high quality corridors, but were still more suitable than the surrounding matrix and could still function to increase connectivity.

This study took place at the Oklahoma State University Botanic Gardens, in an area that was sparse of trees and other vegetation that may provide shade. The study area was regularly mowed to keep vegetation below eight cm in height. Therefore, the matrix provided little cover from direct sunlight and little vegetation to hold moisture, and should have been perceived as "harsh" by the isopods. The matrix was also monitored in each experimental landscape to determine how different soil moisture was from the coco fiber patches and corridors. The "patch" used to monitor soil moisture in the matrix was the same distance away from the release patch as the other target patches, depending on spatial scale, and consisted of matrix only (i.e., no coco fiber mat was present). This area was monitored for isopods, as well as monitored for soil moisture at 2, 4, and 6 cm soil depths. Landscapes were separated by 10 m to reduce the likelihood of isopods dispersing among landscapes, as Grosholz (1993) found the lowest dispersal rates of isopods at this distance. We did not use barriers to prevent isopods from dispersing into other landscapes because we did not want boundaries to be reflective, causing isopods to remain in the system when they would normally have been lost (i.e., left the system).

If trials experienced heavy rainfall that resulted in the entire study area (i.e., patches, corridors, and matrix) to fall in the 8-10 moisture range on a given day during the trial, patches and corridors were still watered. However, low quality corridors were given half the amount of water as the patches and high quality corridors. This was done to ensure that there was still a difference in habitat moisture between the patches and high quality corridors from the low quality corridors and matrix. However, if the matrix soil moisture remained in 8-10 range throughout the majority of the trial (i.e., heavy rainfall at the beginning of the trial saturated the entire landscape to where soil moisture did not lower for multiple days), the data for that trial was removed from the analysis.

One hundred twenty-five isopods were placed in each release patch, based on the average natural population density of isopods/m^2 from Grosholz (1992) (mean: 348.8 isopods/m^2, range: 178-518 isopods/m^2). Before being placed under the release patch, isopods were marked with fluorescent powder. Each replicate landscape was represented by a different color. The powder allowed me to distinguish the released isopods from those that may have recruited to the patches from the surrounding landscape or from another experimental landscape. To confirm that release densities were realistic for this region, I also estimated isopod densities at Lake Sanborn in Stillwater, OK (Table 1). Four transects were created running perpendicular to the lake. A 0.5 x 0.5 m quadrat was placed at 0 m, 5 m, and 15 m distances from the lake in each transect, as long as vegetation or debris did not prevent isopod counts at that distance. When vegetation did prevent counts, the sample for that distance and transect was skipped. Soil moisture was also recorded at 2 cm, 4 cm, and 6 cm within each quadrat.

The dispersal of the isopods was monitored daily for eight days. Grosholz (1993) found that 25-30% of isopods dispersed within eight days, so this should be an adequate trial length. The number of isopods found in the release patch, target patches, and corridors were counted in each experimental landscape. Once an isopod reached a target patch, it was removed from the system to prevent isopods from being re-counted in subsequent days.

In addition to the soil moisture readings that were taken within each experimental landscape, further climate data were gathered for the duration for each trial. These data were obtained from the Oklahoma Mesonet (www.mesonet.org) at the Stillwater station location 36.120930°, -97.095270°. Additional data gathered included days above 32°C, average minimum humidity, rainfall total, and soil temperature. The lethal temperature for the isopod species *Armadillidium vulgare* is 36°C, and it is presumable that temperatures (both air and soil, although soil temperatures are expected to be higher than air temperatures) reaching the lethal limit will influence isopod behavior and habitat preferences. Rainfall and the average minimum humidity level were used since humidity and soil moisture influence the distribution and abundance of isopods, with higher humidity and soil moisture being preferred habitat for the isopods (Warburg 1993).

Objective 2: Evaluate how altering the spatial scale of habitat patches and corridors affects dispersal. Since fragmentation and management decisions occur at many spatial scales, it is important to understand how differences in spatial scale can influence dispersal through corridors. Often, landscape level studies are conducted at a single spatial scale for a multitude of species (Holland et al. 2004). However, different species have different movement abilities that are related to the scale at which a species responds to its environment (Holland et al. 2004). For some species, the scale of patches and corridors and their respective landscape will be appropriate. For other species those same patches, corridors, and landscapes may be larger or smaller relative to the spatial scale at which that species responds to the landscape. For example, Haddad et al. (2003) found that corridors were effective for some butterfly species, but not others. This difference in corridor effectiveness was attributed to the scale of the landscape, which was perhaps too small for some butterfly species to have perceived the corridor as being significantly different than the surrounding matrix. Varying the spatial scale of patch-corridor networks could provide insight into how a species perceives the landscape, and how these changes in scale affect

the utility of corridors. This has important implications for the overall community of organisms present in the landscape, which will include species that perceive the landscape across an extremely broad range of spatial scales.

To determine how modifying spatial scale affects the functionality of corridors, a similar landscape and experimental design as for objective one was used. Habitat patches and corridors consisted of the same coco fiber mat, and were watered and supplemented with food as previously described. Habitat patches and corridors were increased in size by 30% from the normal scale system used for the first objective (to approximately 0.48 m^2 for habitat patches and 0.17 m x 3.3 m for corridors). Distances between the patches were also increased by 30%. Dispersal was monitored in the same manner as previously described.

Statistical Analysis: The numbers of isopods that reached one of the three target patches (at either spatial scale) are considered non-independent because the isopods shared the same release patch and experimental landscape, and once one of the target patches was colonized, the same isopod could not colonize another target patch. My data were also not normally distributed for either Objective 1 or 2, so I used nonparametric statistics. I used Friedman's test to compare the numbers of isopods that reached the different target patches (in other words, how corridor quality affected isopod dispersal). Then I used a Wilcoxon signed rank test as a post-hoc pair-wise comparison test to determine which target patches differed from each other, with corridor quality as the independent variable. Wilcoxon signed rank tests were also performed to evaluate if isopod abundance differed between high and low quality corridors. Finally, a Mann-Whitney U test was performed to evaluate differences in the mean number of isopods that reached the target patches or were present in corridors between normal scale trials and large scale trials. Trials or replicates were removed if extreme conditions (e.g., heavy rainfall, dryness) occurred or if unknown circumstances resulted in the loss of all released isopods in less than 48 hours after the start of a trial.

RESULTS:

Natural isopod densities were estimated near the study area to determine the relevance of release densities, as well as how soil moisture affected natural densities. Isopod density was greatest at a distance of 0 m from the lake in three of the four transects (Table 1). Isopod densities ranged from 0 to 507 isopods/0.5 m^2, with an average density of 99.2 across all the sampling sites. Transect three was the only transect where isopod density increased as distance from the lake increased. As distance from the lake increased, soil moisture tended to decrease. Soil moisture at 2 cm tended to be highest closest to the lake, except for the third transect which had a soil moisture reading of 0 at all distances. Soil moisture trends at 4 cm and 6 cm were not as discernible. Both transects one and four decreased in soil moisture at 4 and 6 cm as distance from the lake increased, but the opposite pattern was observed for transects two and three. Transect three had lowest soil moisture of any transect.

In total, seven normal scale trials were conducted. Four of these were done in 2012 (one in August, two in September, and one in November), and three were done in 2013 (one in May, and two in June). Of the seven total trials, six were used in analyses: three from 2012 and three from 2013 (Table 2). Trial 4 was excluded from the analysis because isopod presences within the experimental landscapes were much lower than in previous trials, with all isopods leaving the system within 48 hours. Soil moisture differences between the release patch and matrix were the most pronounced in Trial 1 and the least pronounced in Trials 3 and 4 (Figure 2). Eight total large scale trials were conducted, all of which were done in 2013. Five trials occurred in July and August, the remaining three trials were done in September and October. Four of the eight trials were included in the analysis (Table 3), three of which were done in July and one of which was done in September. Trial 4 was removed from analysis because a flood interrupted the trial. Trials 5, 6, and 8 were removed from analysis because isopods had completely left the system in all replicates in less than 48 hours, sometimes even less than 24 hours. Soil moisture differences

between the release patch and matrix were the most pronounced in Trials 2 and 4 and the least pronounced in Trials 1 and 3 (Figure 3).

There was a statistically significant difference in the number of isopods that reached the target patches in the normal scale trials, χ^2= 12.44, df = 2, p = 0.002 (Figure 4). There were no significant differences in the number of isopods found in the high quality target patch and the low quality target patch (Z = -0.359, p = 0.720). However, there were significantly fewer isopods in the isolated target patch compared to the high quality target patch (Z = -3.077, p = 0.002), as well as fewer isopods in the isolated target patch compared to the low quality target patch (Z = -2.887, p = 0.004). There was not a statistically significant difference in the number of isopods that reached the target patches in the large scale trials, χ^2 = 2.48, df = 2, p = 0.289 (Figure 4). A post hoc power analysis indicated that my data have little power (normal scale: 8%, large scale: 21%), and therefore may not be able to detect if there was a statistically significant difference between the number of isopods that reached the different quality target patches in either the normal or large scale trials.

A Wilcoxon signed rank test showed that the number of isopods present in the corridors did not statistically differ with corridor quality in the normal scale trials (Z = - 1.541, p = 0.123) (Figure 5). Median isopod numbers in the high and low quality corridors were both 1.00. This was also true of the large scale trials (Z = -0.416, p = 0.677) (Figure 3). For the large scale system, median isopod numbers in the high and low quality corridors were both 0.00. A post hoc power analysis indicated that my data have little power (normal scale: 7%, large scale: 2%), and therefore may not be able to detect if there was a statistically significant difference in isopod presences between the high and low quality corridors at either spatial scale.

The mean number of isopods that reached the high quality target patches in the normal scale trials was statistically significantly higher than in the large scale trials (U = 83, p = 0.05) (Figure 6). There was not a statistically significant difference between spatial scales in the mean number of isopods that reached the low quality target patches (U = 138, p = 0.337) or the isolated

target patches (U = 139, p = 0.280) (Figure 6). When comparing the presence of isopods in corridors, there was not a statistically significant difference between the normal and large spatial scales in the high quality corridors (U = 113.5, p = 0.077) or the low quality corridors (U = 114, p = 0.07) (Figure 7).

Overall, there was low recruitment of isopods from the release patches to the target patches within each landscape in both normal scale and large scale trials (Tables 4 and 5). On Day 1, 125 isopods were released under each release patch. By Day 2, a large portion of these isopods had left the system (i.e., they were no longer under the release patch, the corridors, target patches, or in the surrounding matrix). The normal scale trials had a reduction in isopod numbers from 73.6 – 93.6% (mean = 84%), while the large scale trials had a reduction in isopods between 64.8 – 96% (mean = 82.8%). Isopods continued to leave the system after Day 2, but at a much lower rate. After Day 4, isopods were absent from release patches in several landscape replicates, and this continued for the remainder of the trials. There were few trials where isopods remained in the release patch by Days 7 and 8 in both normal and large scale trials.

The 2012 normal scale trials all contained at least one day where the temperature reached 32°C or higher (Table 2). Two of the 2012 trials had at least half of their duration comprised of high temperatures above 32°C. This was also the situation for the 2013 normal scale trials: all trials had at least one day when the maximum temperature reached 32°C, and more than half of the days reached 32°C in two of the trials. In 2012, the average minimum humidity remained above 25% and stayed below 50%. The average humidity during the 2013 trials stayed above 40% and below 60% (Table 2). 2013 trials received more rain (total for all three trials 10.5 cm in 2013 versus 4.23 cm in 2012) than the 2012 trials. The average soil temperature ranged from 20-28°C for all trials. Three trials had an average soil temperature in the range of 20-25°C, while the other three were in the range of 26-28°C.

Of the four large scale trials, three had at least six days above 32°C (Table 3). The average minimum humidity for Trials 2, 3, and 7 ranged from 41-46%; Trial 1 had an average

minimum humidity of about 32%. Trials 1 and 3 had below one cm of total rainfall, while Trials 2 and 7 received 3.15 and 5.31 cm, respectively.

DISCUSSION:

There was a significant difference in the number of isopods that reached the target patches during the normal scale trials, with more isopods reaching the patches connected by high or low quality corridors than the isolated patches. However, there was no statistically significant difference between the numbers of isopods which reached patches connected by low and high quality corridors. I expected that the target patches connected by high and low quality corridors would receive higher numbers of isopods than the isolated target patches, since the isolated patch was surrounded by the matrix. The lack of a difference in the numbers of isopods reaching patches connected by high and low quality corridors could suggest that low quality corridors may be just as effective at increasing dispersal as high quality corridors, at least under some conditions. However, post hoc power analysis indicated that my data had little power, so it may be that there was a difference between the numbers of isopods to reach the low and high quality target patches, but my sample size was not adequate to detect that difference. However, there are some situations where low quality corridors may function as well as high quality corridors. For example, Jenkins et al. (2006) suggest that corridors between aquatic and terrestrial habitats could effectively increase connectivity for salamanders, especially juveniles. The authors suggest that the corridors might not have to consist of mature, close-canopy forest, as long as they provide adequate cover and microclimate conditions conducive to the target species and relevant life stages.

At the large spatial scale, there was no statistical difference in the numbers of isopods which reached the isolated patch compared to the patches connected by high or low quality corridors. Habitat fragmentation occurs at multiple spatial scales, and different species respond to the landscape (and habitat fragmentation) at different scales. Therefore, the spatial scale of

corridors may be too small or too large for some species in the community, and these species may respond differently to corridors at different scales. This may be true for other landscape elements as well. For example, if a corridor is large relative to the spatial scale at which a species responds to the landscape, then that species may use the corridor as habitat and not perceive it as a corridor. Haddad (2003) found that corridors were beneficial for some species of butterflies but not others and attributed this to scale being too small for some butterfly species to discern the difference between the corridor habitat and the matrix habitat. However, it is likely that environmental conditions influenced my results, which may limit their usefulness for describing corridor use at different spatial scales for isopods. Isopods may have been better able to travel through the matrix during the large scale trials due to the higher amounts of rainfall during this time period, which likely increased humidity levels within the experimental landscapes.

There was no statistically significant difference in the numbers of isopods present in the high and low quality corridors during both the normal and large scale trials. This could suggest that isopods may be using high and low quality corridors equally. However, a post hoc power analysis indicated little power to my data, so it is not possible to discern if there was truly not a significant difference between isopod presences in low and high quality corridors. Low quality corridors could be useful in situations where the land has been too heavily converted to restore. For instance, it would not be possible to restore old-growth forested corridors to increase connectivity between isolated forest patches over the short term. However, alternative approaches that provide cover and the appropriate microclimate may work for some species (e.g., Jenkins et al. 2006). In this situation, it may be possible that a corridor with younger trees and shrubs would provide adequate connectivity for salamanders.

When comparing the proportion of isopods that reached the target patches between the normal and large spatial scale trials, there was not a statistically significant difference in the proportion of isopods that reached the low quality target patches or the isolated patches (Figure 4). In addition, there was also not a significant difference in the proportion of isopods present in

the low quality or high quality corridors between the spatial scales (Figure 5). There was, however, a statistically significant difference in the proportion of isopods that reached the high quality target patches (Figure 6). Fewer isopods may have reached the target patches at the larger spatial scale because 1) fewer isopods may have left the release patches, 2) isopods may have remained in corridors (i.e., used corridors as habitat), or 3) because it may take longer for isopods to reach the target patches because of the increased spatial scale. The first explanation seems unlikely because the numbers of marked isopods left in the release patch at the end of the trials were consistently low. We also did not find a difference in the number of isopods within the high and low quality corridors between the spatial scales, suggesting the second and third explanations are unlikely as well. In this system it may be that *A. vulgare* has too great of dispersal capabilities to see a difference in corridor use at the larger spatial scale, or that other extreme environmental conditions influenced the observed patterns, either through modifying the dispersal behavior of isopods or influencing their behavior in other ways.

At the beginning of this study, natural isopod densities were estimated to assess if the population densities of isopods near my study location were comparable to those of the Grosholz (1992 and 1993) studies. These data also provide a framework for evaluating if density dependent effects could have influenced the results. Grosholz (1992) found average natural population densities of isopods to be 348.8 isopods/m^2 (range 178-518 isopods/m^2). In my study, I found a mean of 209.25 isopods/0.5 m^2 (range 9-507 isopods/0.5 m^2) or 837 isopods/m^2 (range 36-2,028 isopods/m^2). The average isopod densities found near my study site were higher than the natural population densities that Grosholz (1992) found for his study, but likely reflected the large amount of woody debris (i.e., cover and increased moisture for isopods) located at my sampling site, which was selected because it was a very suitable area for isopods. Therefore, my release density of 125 isopods/0.36 m^2 is within the normal range for isopods in the study area, and should have been low enough to avoid issues such as increased dispersal due to density dependent factors if unnaturally high densities had been used.

Trials at both spatial scales had at least one day where the temperature reached 32°C, and many had multiple days that reached this temperature. Higher temperatures will likely influence the behavior and survival of the isopods. Average soil temperatures were commonly between 25-28°C. However, these numbers are likely conservative to what the isopods were actually experiencing, since the soil temperatures recorded by the Oklahoma Mesonet were taken at ten cm below ground level. With these many days with temperatures nearing the lethal temperature for *A. vulgare*, as well as likely even higher soil temperatures experienced by the isopods, it is probable that this had a large influence on usage of the experimental landscapes in my trials.

Throughout all of the trials, large numbers of isopods left the system between Days 1 and 2 (Tables 4 and 5) and continued to leave the system for the remainder of the trial, albeit in lower numbers. Low usage of the landscapes may be due to several factors. Landscapes were in direct sunlight for the entire day. Originally I expected this to increase the difference between the artificially created habitat and the surrounding matrix, which should have encouraged isopods to remain within the experimental landscapes. However, this may have resulted in high temperatures within the overall landscapes. Released isopods may have left the landscapes as the lethal temperature (36°C) was approached, moving to drier areas to regulate body temperature via evaporative cooling. While humidity and moisture play an important role in isopod population densities and habitat selection, when temperatures begin to reach lethal limits, temperature may play a more important role than humidity or moisture (Cloudsley-Thompson 1956). *Armadillidium vulgare* may also be more active at higher than lower temperatures. Cloudsley-Thompson (1956) found that *A. vulgare* was more active by 20% at 30°C than at 18°C. At 18°C, only 1.2% of *A. vulgare* were moving in comparison to 24.2% that were moving at 30°C. This overall greater activity may have also contributed to the large drop-offs in isopod presences within experimental landscapes.

Post hoc power analyses indicated that my data have little power to discern if there really was a difference in the usage of low and high quality corridors by isopods. Low power may be

due to small sample size, but could also reflect the low usage of the experimental system by isopods, which may have been influenced by extreme weather conditions. Further work should be done to evaluate if there are differences in dispersal between high and low quality corridors.

Isopods were not allowed to leave experimental landscapes in Grosholz's studies because he placed aluminum flashing 12 cm below ground level to prevent departure. I chose not to use aluminum flashing because having a boundary around habitat patches and corridors would not be realistic to what organisms would encounter in their natural habitat and isopods "bouncing back" from landscape boundaries would produce unrealistic results (i.e., potentially artificially high use of the patches and corridors). In his study, Grosholz (1992) was evaluating the effects of competition on virus prevalence, and wanted to prevent any additional isopods from recruiting to the system. Forcing isopods to remain within my system would have “forced” the isopods to use the system, and may have further skewed the numbers of isopods that used the patches and/or corridors. Isopods could have repeatedly moved back and forth between the target patches using the corridors, or, once they hit the barriers, reflected back into the target patches without using the corridors.

Predators may also have influenced isopod behavior in my trials, although I think this is unlikely. Known predators include ants and spiders (Warburg 1993), as well as carabid beetles, birds (specifically the European Starling), and some amphibians and reptiles (Cole 1946, Hamilton and Pollack 1961, Paris 1963). Many of these organisms occurred within the overall study area (i.e., the OSU Botanic Garden), and spiders, ants, and carabid beetles were frequently found under patches and corridors. I observed ants carrying experimental isopod carcasses (i.e., marked with fluorescent powder) during some preliminary trials at a different site, which is one of the reasons I did not use that site. However, I do not think predation is what caused the large drop off in numbers during my experiments, as most studies have found that isopod populations, especially *A. vulgare,* are not heavily influenced by predation (Paris 1963, Warburg 1993). Low

predation may be attributed to *A. vulgare*'s ability to roll into a ball when threatened, or that they are distasteful to predators due to a secretion from the tegumental glands (Paris 1963).

Although my data were inconclusive due to low power, low quality corridors may be as effective, or in some cases more effective, than high quality corridors for a variety of reasons. Organisms using low quality corridors may reach connected patches more quickly than those using high quality corridors. Movements typically become faster and more direct in a hostile matrix environment (Hodgson et al. 2011), which can lead to increased dispersal distances. Habitat that is perceived by an organism as lower quality than preferred habitat may encourage quicker movements. Organisms using high quality habitat corridors may move more slowly, or may remain in high quality corridors and use them as habitat instead of a movement conduit.

Habitat quality in corridors may not need to be the same as preferred habitat to increase dispersal. For instance, different types of matrices may facilitate or impede movement (Baum et al. 2004). It is generally thought that a matrix that is structurally similar to an organism's habitat will facilitate movement and a matrix that is structurally different will hinder movement (Stamps et al. 1987, Noss and Cooperrider 1994, Laurance et al. 2002). If the matrix is perceived as impermeable to an organism, it is likely that a low quality corridor that is of higher quality than the surrounding matrix may be useful in increasing dispersal, even if not the preferred habitat of the species.

In some situations low quality corridors may be more beneficial than high quality corridors, such as if high quality corridors act as an ecological sink. For example, organisms may use a high quality corridor as habitat, never reaching the intended connected patch. As a habitat patch, corridors have high amounts of edge, which can increase edge effects, including increased predation and/or parasitism (Hess and Fischer 2001). This can also be a factor if organisms move more slowly through a high quality corridor, increasing the likelihood of predation or other negative factors associated with increased amounts of edge (Soule and Gilpin 1991, Sisk and Margules 1993, Breininger et al. 2006).

The success of corridors, regardless of quality, will be influenced by many factors. For instance, not all species will use corridors, and their benefits may be greater at certain life stages than at others. What one species perceives to be a suitable movement conduit may not be perceived as suitable to another. Species that are edge sensitive may avoid corridors, depending on their width. Under these circumstances, the quality of the corridor may not matter. For example, a study that evaluated the optimal width for corridors found that voles would not enter the corridor of the smallest width, most likely due to behavioral aversion to edges (Andreassen et al. 1996). Another study involving amphibians found that juvenile salamanders exhibited behavioral avoidance and possibly higher mortality rates in old-agricultural fields compared to forest (Rothermel and Semlitsch 2002). In situations such as these, corridors may be more beneficial for juveniles than other life stages. Therefore, surrounding land use as well as climatic conditions and life stage can influence corridor use.

The matrix can also influence the usage of corridors, and low or high quality corridors may be more or less effective depending on matrix type. For instance, birds used corridors more frequently when the adjacent matrix was completely clear-cut in comparison to a matrix that was selectively logged (Rosenberg et al. 1997). Baum et al. (2004) found in a matrix that supports high-rates of interpatch dispersal for planthoppers (i.e., a low-resistance matrix), both stepping stones and corridors promoted high connectivity, increasing the number of planthopper colonists threefold in comparison to target patches surrounded by matrix only. However, in a high-resistance matrix corridor effectiveness declined (compared to in the low-resistance matrix), and stepping stones did not increase dispersal at all compared to isolated target patches, likely due to the number of edges that needed to be crossed. Corridor effectiveness can also vary over time. For example, Rosenberg et al. (1997) found that after several weeks without rain, salamanders were more likely to reach patches connected by corridors than unconnected patches. In addition, salamanders that were found in the matrix between isolated patches experienced weight loss and increased rates of mortality.

When applying results from model systems to real world scenarios, traits of the model organism versus the target conservation species should be considered. For instance, is the model organism a generalist or a specialist? Does it have low or high dispersal capabilities? Facilitating movement of generalist species, such as the red fox or coyote, can be easier than for specialist species. However, edge effects may influence the availability resources for generalist species as well. For example, Mills (1996) suggested that red backed voles may prefer interior habitat not because they have a behavioral avoidance of edges, but because the abiotic conditions in the interior of the forest were more likely to increase the growth of fungi, which is a preferred food item for the voles. Specialists may also be more sensitive to invasive species, or human influence, another aspect to consider when creating corridors for certain species, since it is possible that corridors could increase connectivity for invasive species (or disease organisms) as well.

In general, isopods are considered generalists, which influences how the results from my study can be applied to other species and systems. Isopods do not seem edge sensitive, and therefore readily cross habitat-matrix boundaries and may not remain in habitat patches and/or corridors as much as species less likely to cross edges. Isopods also seem to have relatively strong movement abilities, so leaving the system to find new habitat may not have been have been deterred by movement capabilities. Since they are omnivorous (specifically, detritivores), food might not influence behavior or encourage corridor use as much as for other species with more restrictive food requirements. When applying these results to other systems, it is important to consider other factors that may influence the use of corridors, such as the extreme temperatures that isopods experienced in my experimental landscapes. Similar patterns would be expected for other desiccation sensitive organisms, such as amphibians, which also require adequate cover to prevent desiccation and regulate temperature.

Further studies should be done to evaluate the effectiveness of low quality corridors in increasing connectivity between isolated habitat patches. Specific to my model design, it would be beneficial to conduct the study in with different matrix types and under different

environmental conditions (e.g., normal rainfall, drought). Isopods were likely impacted by the high temperatures common to Oklahoma summers as well as direct sunlight on the experimental landscapes. Conducting this study in a shaded area (e.g., location of natural isopod density study at Lake Sanborn) or at a time of year when temperatures were not as extreme, could yield different results. Studies of low quality corridors, should examine a wide range of different taxa, including habitat generalists and specialists. Different ways of modifying corridor quality should also be evaluated as relevant to the study species. As humans continue to develop land, and habitat fragmentation and loss continue, increasing connectivity will be critical for mitigating the detrimental effects of fragmentation. Assessing all means to increasing connectivity within a landscape will be necessary, as it is not always possible to retain or restore high quality habitat corridors. Low quality corridors could be one way to increase connectivity, and the efficacy of low quality corridors should be further studied.

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Figure 1. Each experimental landscape consisted of a release patch (normal scale: 0.36 x 0.36 m, large scale: 0.48 x 0.48 m), where isopods were released on the first day of the trial. Three target patches were placed 2.5 m from the release patch and connected with a high or low quality corridor (normal scale: 0.13 x 2.5 m, large scale 0.17 x 3.3 m) or left unconnected. Dashed lines represent an area where no patch was placed, but was inspected to assess isopod presence in the matrix.

Figure 2. Average soil moisture readings (mean ± SE) of release patches and representative matrix patches (dashed patch in Figure 1) in the normal scale trials.

Figure 3. Average soil moisture readings (mean ± SE) of release patches and representative matrix patches (dashed patch in Figure 1) in the large scale trials.

Figure 4. Total number of isopods (mean ± SE) in the target patches over the length of the trial.

Figure 5. Total number of isopods (mean ± SE) present in the corridors over the length of the trial.

Table 1

Distance from lake (m)	Transect*	Isopod density (per $0.5m^2$)	Soil moisture 2 cm	Soil moisture 4 cm	Soil moisture 6 cm
0	1	507	5	6	8
0	2	253	7	6	7
0	3	9	0	1	3
0	4	68	9	10	10
5	1	6	0	1.5	6
5	2	72	5	8	10
5	3	15	0	0	1
5	4	23	0	2	8
15	1	0	0	0	2.5
15	3	42	0	1	4

* Transects 2 and 4 at distances 15 m from lake were not included because the amount of vegetation within the area was too dense to accurately count isopods.

Table 2

Year	Trial number	Date	Days above 32°C	Average min. humidity (%)	Rainfall total (cm)	Average soil temperature (°C) (10 cm)
2012	**1**	8/15-8/22	6	25.8 ± 2.6	0.5	26.3 ± 0.25
2012	**2**	9/11/-9/18	4	46.8 ± 8.3	1.83	23.3 ± 0.66
2012	**3**	9/25-10/2	1	40.1 ± 7.7	1.9	22.8 ± 0.46
2013	**5**	5/17-5/24	1	60.1 ± 4.9	3.66	20.2 ± 0.39
2013	**6**	6/11-6/18	5	47.8 ± 4.1	6.2	25.9 ± 0.26
2013	**7**	6/21/-6/28	8	41.8 ± 3.1	0.64	27.4 ± 0.32

Table 3

Year	Trial number	Date	Days above 32°C	Average min. humidity (%)	Rainfall total (cm)	Average soil temperature (°C)
2013	**1**	7/2-7/9	6	31.6 ± 1.9	0	26.4 ± 0.39
2013	**2**	7/9-7/16	6	45.9 ± 5.3	3.15	27.3 ± 0.47
2013	**3**	7/16/-7/23	8	44.8 ± 1.9	0.71	27.5 ± 0.33
2013	**7**	9/27-10/4	2	41.6 ± 3.1	5.31	22.5 ± 0.42

Table 4

Trial - Replicate *	Day 2	Day 3	Day 4	Day 5	Day 6	Day 7	Day 8
1 - 2	32	24	4	-	-	-	-
1 - 3	27	25	9	3	-	-	-
2 - 1	25	17	10	10	7	6	3
2 - 2	13	13	9	5	3	3	1
2 - 3	29	16	14	11	11	8	-
3 - 1	11	7	7	4	3	-	-
3 - 2	24	15	6	5	4	-	-
3 - 3	14	12	7	2	-	-	-
3 - 4	8	4	2	-	-	-	-
5 - 1	22	5	4	2	2	-	-
5 - 2	31	14	9	4	4	-	-
5 - 3	14	12	5	3	1	-	-
5 - 4	17	13	4	3	1	-	-
6 - 1	8	8	6	4	-	-	-
6 - 2	20	7	7	-	-	-	-
6 - 3	33	19	3	-	-	-	-
6 - 4	30	8	4	-	-	-	-
7 - 1	12	10	7	6	3	-	-
7 - 2	25	13	6	4	2	2	-
7 - 3	20	11	8	3	2	1	-
7 - 4	19	15	8	5	-	-	-

* Trials removed because of extreme weather included Trial 1.

Table 5

Trial – Replicate *	Day 2	Day 3	Day 4	Day 5	Day 6	Day 7	Day 8
1 - 1	29	27	10	5	2	1	-
1 - 2	25	17	16	3	-	-	-
1 - 3	26	20	17	3	1	-	-
1 - 4	44	28	17	14	-	-	-
2 - 1	16	15	5	3	1	1	1
2 - 2	19	12	11	5	4	-	-
2 - 3	19	4	-	-	-	-	-
2 - 4	16	14	4	3	2	-	-
3 - 1	22	13	4	7	3	1	-
3 - 2	20	10	1	1	-	-	-
3 - 3	13	9	3	6	-	-	-
3 - 4	22	11	9	4	3	-	-
7 - 1	25	5	2	-	-	-	-
7 - 2	5	3	3	-	-	-	-
7 - 3	28	2	1	-	-	-	-
7 - 4	15	12	5	-	-	-	-

* Trials removed because of extreme weather included all replicates within Trials 4, 5, 6, and 8.

Figure 1

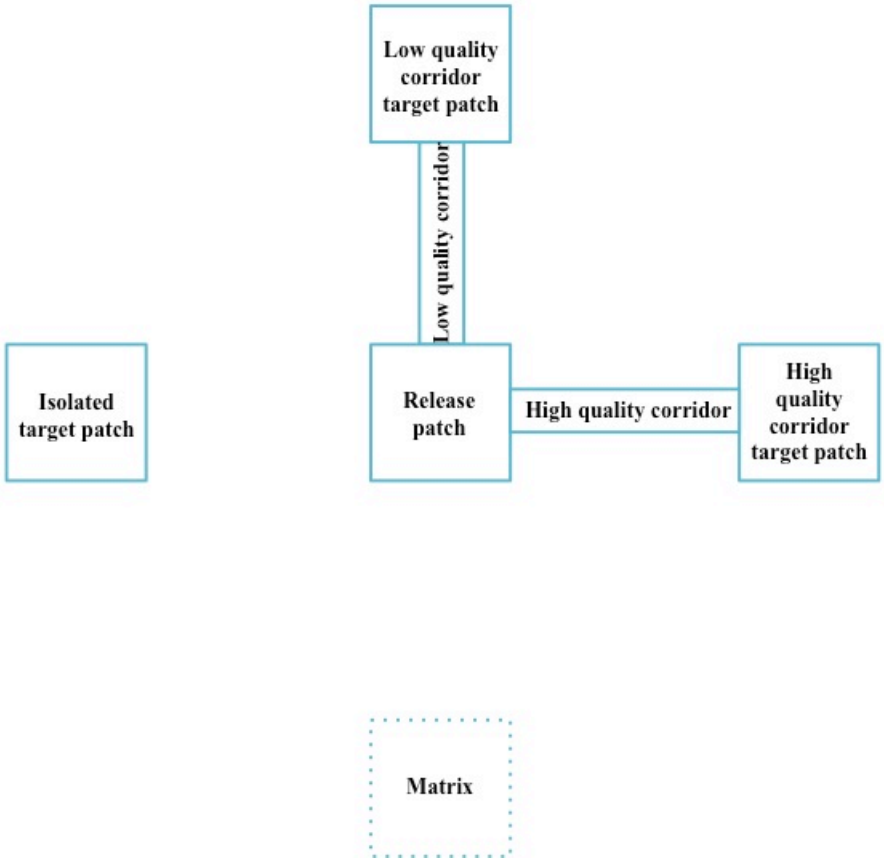

Low quality corridor target patch
Low quality corridor
Isolated target patch
Release patch
High quality corridor
High quality corridor target patch
Matrix

Figure 2

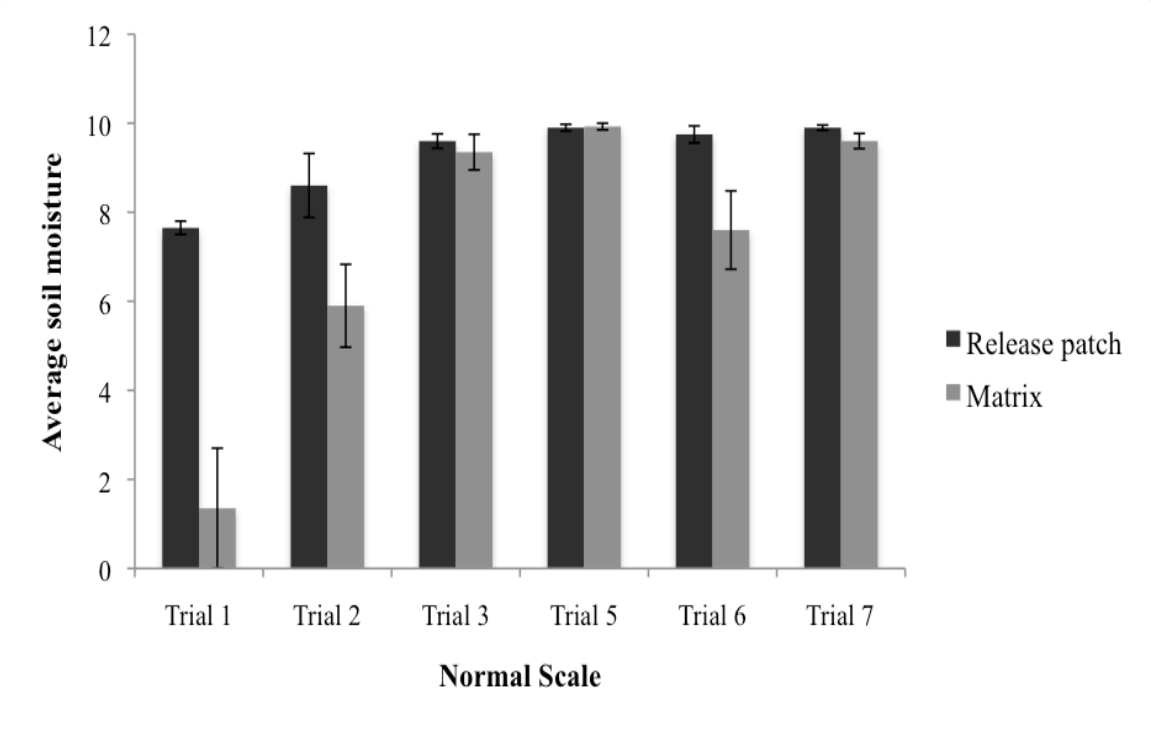

12
10
8
6
4
2
0
Average soil moisture
Trial 1
Trial 2
Trial 3
Trial 5
Trial 6
Trial 7
Normal Scale
Release patch
Matrix

Figure 3

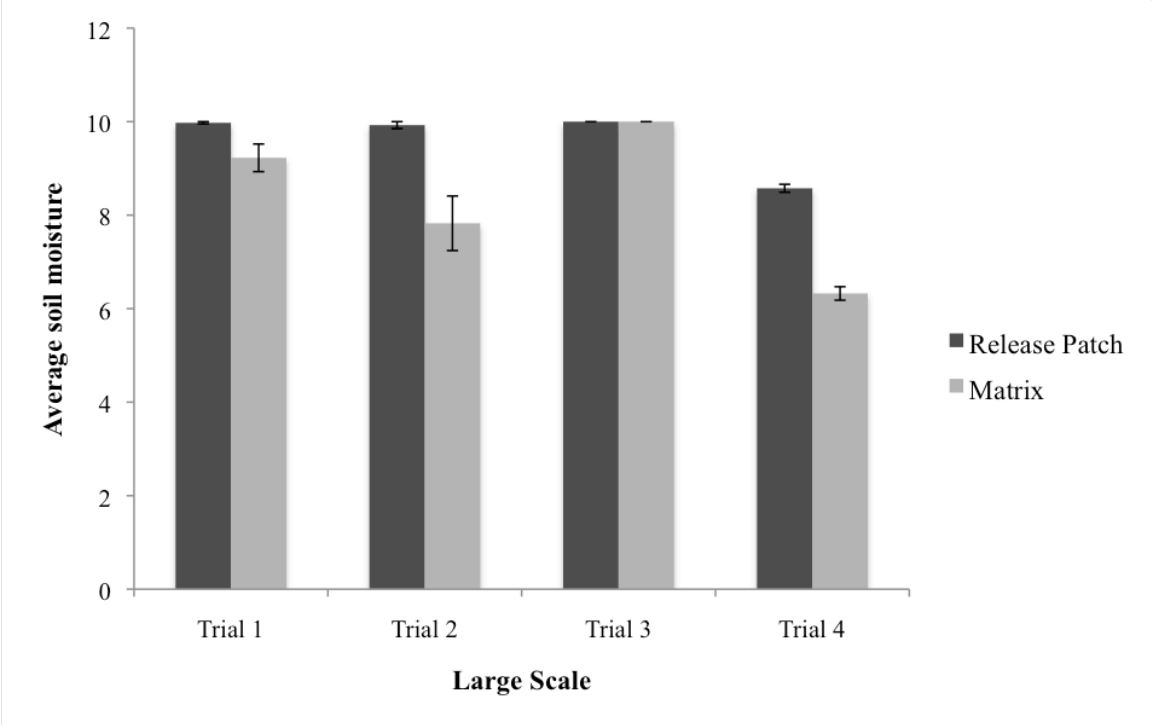

12
10
8
6
4
2
0
Average soil moisture
Trial 1
Trial 2
Trial 3
Trial 4
Large Scale
Release Patch
Matrix

Figure 4

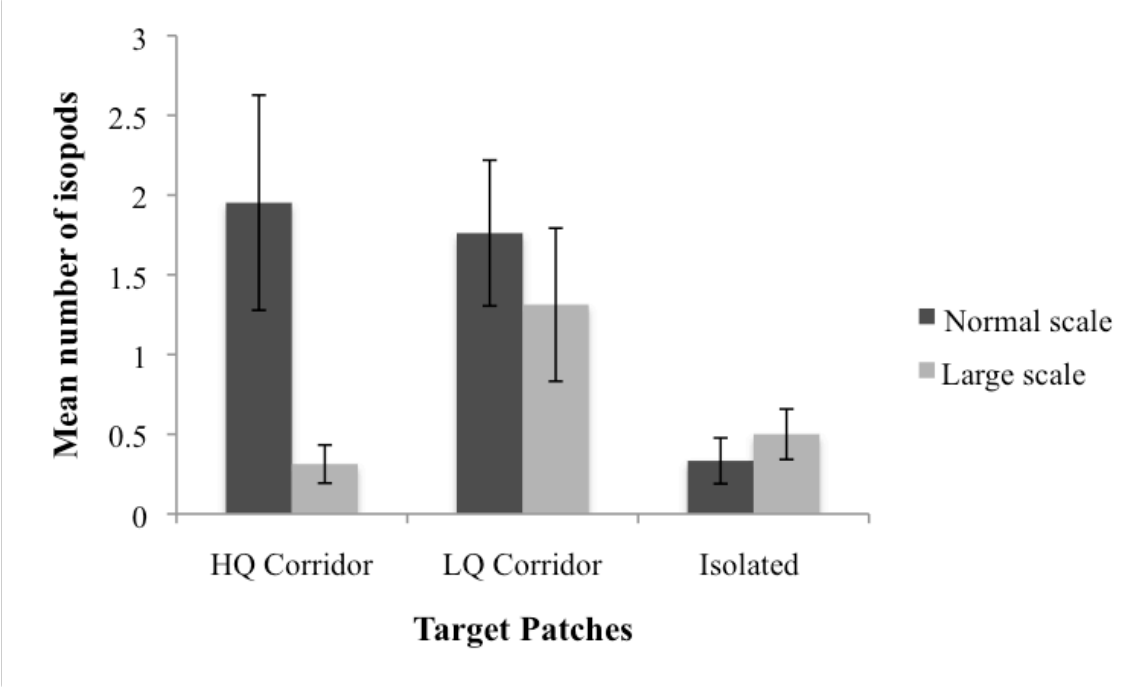
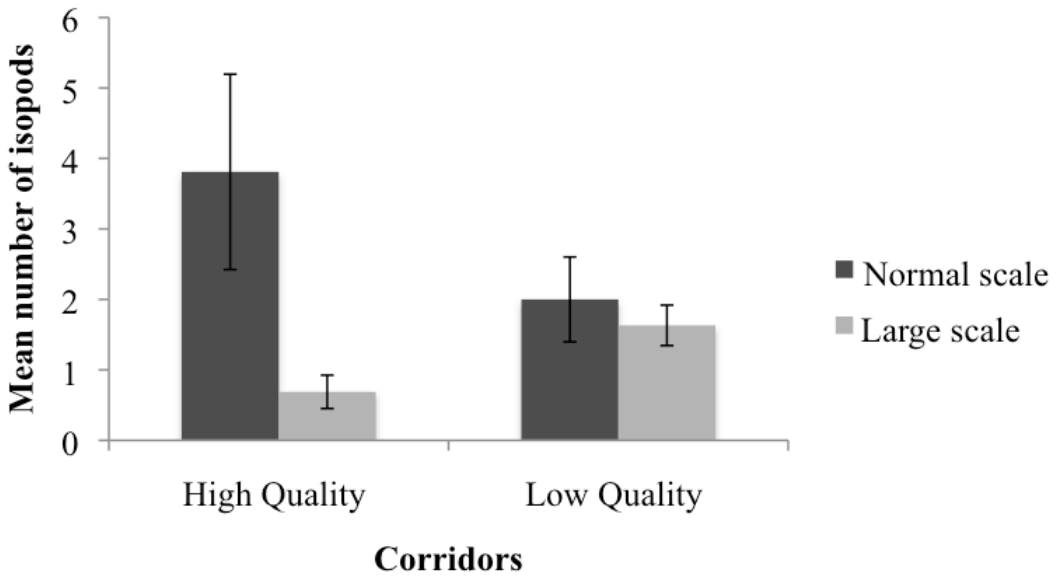

Mean number of isopods
3
2.5
2
1.5
1
0.5
0
HQ Corridor
LQ Corridor
Isolated
Target Patches
Normal scale
Large scale

Figure 5


Mean number of isopods
6
5
4
3
2
1
0
High Quality
Low Quality
Corridors
Normal scale
Large scale

VITA

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